

***PHILOPONELLA REPUBLICANA* (ARANEAE, ULOBORIDAE) AS A COMMENSAL IN THE WEBS OF OTHER SPIDERS**

Ann L. Rypstra and Greta J. Binford¹: Department of Zoology, Miami University,
1601 Peck Blvd., Hamilton, Ohio 45011 USA

ABSTRACT. Juvenile individuals of the spider species, *Philoponella republicana*, were common in the webs of the social spider, *Anelosimus eximius*, and the solitary spider, *Architis* sp., in the forest habitats of the SE Peru. The abundance, size and location of *P. republicana* individuals were surveyed in each host web. Although the host webs were similar in size and conformation, more *P. republicana* individuals were found in the social spider webs than in the solitary host webs. Likewise, the number of *P. republicana* in the social spider webs was correlated with host web size. The mean size of prey captured by *P. republicana* was 2.1 mm, which was significantly smaller than the prey taken by the social spider, and, in feeding trials, *Architis* sp. individuals reacted only infrequently to prey of that size. This separation in the size of prey taken caused us to conclude that *P. republicana* acted as a commensal for the most part; however, they were observed to prey on the social spiders occasionally. Small *P. republicana* were the most common in both host webs and tended to be high in the barrier webbing. The largest individuals in the social host webs were located under the sheet area, and these individuals were observed to feed more frequently than spiders in other size classes and in other areas of the host webs. We conclude that juvenile *P. republicana* are commensals in both host webs but that they benefit more from the greater amount of activity in webs of the social spiders.

Mounting evidence from phylogenetically diverse species shows that grouping behavior may simultaneously reduce individual risk of predation and enhance feeding efficiency (Pulliam & Caraco 1984; Uetz 1988; Uetz & Heiber 1994). Heterospecific interactions within social groups can bring advantages to individuals in those groups that do not accrue to individuals in single species aggregations (Morse 1970; Barnard & Thompson 1985). Slightly different foraging modes and food preferences may lead to more efficient resource usage by mixed species groups which can simultaneously take advantage of other kinds of advantages of being in a group.

A wide variety of heterospecific relationships have been reported among spider species ranging from predation (Larcher & Wise 1985; Jackson & Whitehouse 1986; Jackson 1990) to kleptoparasitism (Vollrath 1987; Cangialosi 1990), to commensalism (Rypstra 1979; Bradoo 1986, 1989). In many of these instances, host spiders have large complex webs that can provide a living space with some support and protection for the second spider species (Rypstra 1979; Bradoo 1986, 1989; Hodge & Uetz 1992). In particular, the webs of communal or social spiders tend to provide habitat for other spider species who in-

teract with the host in both positive and negative ways (Rypstra 1979; Bradoo 1989; Cangialosi 1991; Hodge & Uetz 1992).

A commensal association occurs when one species reaps some benefits by association with a host species but the host species is essentially unaffected, positively or negatively, by the association. Commensalism has been reported with some frequency among spider species in the family Uloboridae (Struhsaker 1969; Opell 1979; Bradoo 1986; 1989). Bradoo (1989) concludes that *Uloborus ferokus* Bradoo (Araneae, Uloboridae), living in the webs of the social spider *Stegodyphus sarasinorum* Karsch (Araneae, Erisidae), receives protection, support and increased prey capture which increases its lifespan and fitness. The spider species, *Philoponella republicana* (Simon) (Araneae, Uloboridae), is frequently found in single species aggregations (Smith 1985; Binford & Rypstra 1992); but, in addition, we have found immature individuals of the species in the interstices of the webs of almost all complex, semi-permanent spider webs at our study area in SE Peru. *P. republicana* were particularly common in the webs of *Anelosimus eximius* Simon (Araneae, Theridiidae), a cooperatively social species in this area. The goal of this

¹Present address: Dept. of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721 USA

study is to describe the abundance and distribution of *P. republicana* in the large webs of this social spider in comparison with its distribution in the webs of a solitary species, *Architis* sp. (Araneae, Pisauridae), whose web is of similar size and structure (Nentwig 1985).

METHODS

Data were collected on spider populations inhabiting the subtropical moist forest of the Tambopata Reserved Zone, 35 km southwest of Puerto Maldonado in Madre de Dios, Peru. Data were collected in the dry season: July and early August of 1987, 1988 and 1989 (see Erwin 1985 for complete description of the habitats).

The webs of both host spiders were very similar in overall appearance. They consisted of a dense sheet of webbing subtended by a maze of barrier webbing encompassing neighboring vegetation (Brach 1975; Christenson 1984; Nentwig 1985). *A. eximius* is a cooperatively social species so each web contained several hundred to several thousand individuals that worked together to capture prey (Brach 1975; Christenson 1984). *Architis* sp. is a solitary spider and a single individual monitors insects arriving in the web from a funnel-shaped retreat at one end of the sheet area of the web (Nentwig 1985). Adults of *A. eximius* are 4–6 mm in length, which is substantially smaller than *Architis* adults which are 8–12 mm in length.

Surveys were conducted of all *A. eximius* webs found, a total of 46 webs, between 4 July and 4 August in 1987 (18 webs), 1988 (16 webs) and 1989 (12 webs). To avoid the confounding factor of repeated measures only one survey per social spider web was included in the data set. In order to standardize for season and temperature across the years we selected the first survey conducted on a web after 4 July on a dry day on which the temperature was between 24–28 °C. A total of 12 *Architis* sp. webs were surveyed a single time and under similar weather circumstances in July of 1989. During each survey, *P. republicana* were classified into three size categories: large (4–6 mm in length), medium (2–4 mm in length), and small (less than 2 mm in length). *P. republicana* were also categorized by position in the host web. That categorization included spiders located under the sheet, just above the sheet (within 2 cm), in the low barrier of the web (2–20 cm above the sheet) and in the high barrier (20 cm or more above the sheet).

In order to obtain one measure of site quality

within the host web, we also attempted to determine the feeding frequency of *P. republicana* spiders located in different positions. A spherical bundle in the chelicerae of the spider was evidence that it had captured a prey item recently. One complication that arises in determining the likelihood of feeding is that the spider will feed longer on large prey than on small prey so a survey sampling technique would have biased the results toward large prey. In the case of *A. eximius* webs, we typically spent two or more hours observing so, for this study, we only counted the prey items that were captured during our observation times. For *Architis* webs, we surveyed a second time 2–3 hours after the first observation to estimate a feeding rate in a similar fashion.

To determine whether the two species were actively competing for prey that entered the web or if there was a division of resources based on prey size, we needed to determine the range of prey sizes taken by each of the host species. The distribution and frequency of prey capture were obtained for *A. eximius* in the course of a simultaneous study (Rypstra 1990; Rypstra & Tirney 1991). In order to determine whether the solitary *Architis* sp. actively preys on insects in the size class that *P. republicana* handles, we conducted a feeding experiment. Field-caught fruit flies (*Drosophila* spp. 1.5–2.0 mm in length, the mean size of prey taken by *P. republicana*) were gently blown into each of ten webs of *Architis*. In all cases the *Architis* individual was at the opening of its retreat in a feeding position at the time the prey were introduced. If the *Architis* spider retreated before the prey was in the web or if it was apparent that we had disturbed her in the process, no data were taken. If we successfully introduced the fly without disturbing the host spider and we were able to detect that the fly contacted the sheet in a way sufficient to vibrate the threads, we recorded the reactions of the *Architis*. Between 8–12 flies were tested in each of ten *Architis* webs. After each trial, a larger fly or grasshopper was introduced into the web to see if the host spider was receptive to any prey. If we could not get the spider to respond, the results of the trial were excluded from the analysis.

RESULTS

All of the webs that we found in all three years had some *P. republicana* in them. On average, there were 8.4 ± 3.3 (mean \pm standard deviation)

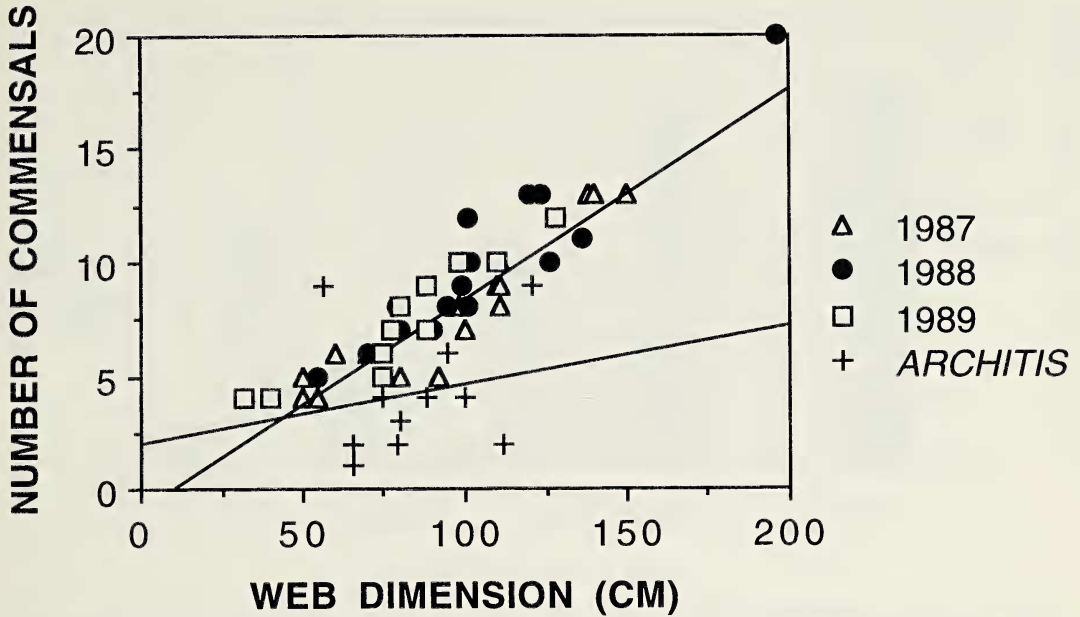


Figure 1.—The number of commensal *Philoponella republicana* individuals vs. the longest horizontal dimension of the host web. Data points indicated for the three years (1987, 1988, and 1989) are all for the social host, *Anelosimus eximius*. Data for the solitary host, *Architis* sp., were all gathered in 1989. The correlation between web size and number of commensals is significant for the social *Anelosimus eximius* but is not significant for the solitary *Architis* sp.

P. republicana individuals in the 46 *A. eximius* webs we surveyed over three years. There were no differences among the years (Kruskal-Wallis Multiple Comparisons, $P > 0.05$). There were significant positive relationships between social spider web size and the number of *P. republicana* in the web both within each year and when the data for all years were pooled. The strongest relationship was between the longest horizontal dimension and number of spiders (for all years together: Spearman's $r = 0.85$, $P < 0.05$) (Fig. 1).

We found a mean of 4.17 ± 2.6 *P. republicana* individuals in the 12 webs of *Architis* sp. that we surveyed in 1989. This was significantly less than the numbers we found in the social spider webs (Mann-Whitney *U*-Test, $P < 0.05$). The webs of *Architis* and *A. eximius* were similar in all the dimensions we measured: longest horizontal, perpendicular or web height, and height of the sheet above ground (Mann-Whitney *U*-Test for all, $P > 0.25$). However, there was no relationship between web size and number of *P. republicana* individuals in *Architis* sp. webs (longest horizontal web dimension and spider number: $r = 0.4$, $P > 0.2$) (Fig. 1).

The distribution of *P. republicana* individuals in the various size classes we identified was not even within either host web (χ^2 Test, $P < 0.05$). In both web types, small spiders were most abundant and large spiders the least abundant (Fig. 2). The size distributions of *P. republicana* in the two host types were significantly different from one another (χ^2 Test, $P < 0.05$). Most noticeably, there were more large individuals in *A. eximius* webs than there were in the webs of *Architis* sp. (Fig. 2). The distribution of *P. republicana* webs across the four positions we identified in the host webs was also skewed (χ^2 Test, $P < 0.05$). In *Architis* sp. webs, most of the *P. republicana* (40 of 63 total) were located in the barrier area (Fig. 3). However, in *A. eximius* webs, *P. republicana* were evenly distributed between areas close to the sheet and barrier areas (Fig. 3). Specifically, the *P. republicana* in the social spider webs were most abundant under the sheet and in the high barrier; and they were least abundant just above the sheet and in the low barrier (Fig. 3). The distributions of *P. republicana* webs in the two host species we observed in 1989 were significantly different from one another (χ^2 Test, $P < 0.05$).

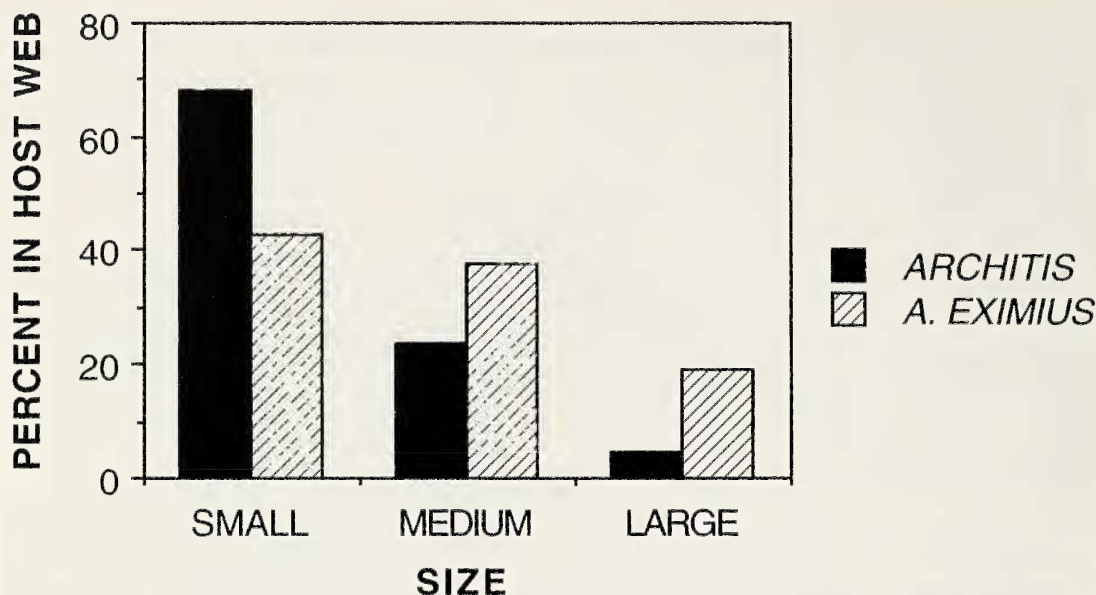


Figure 2.—The size distribution of *Philoponella republicana* individuals in the webs of the two host species, *Architis* sp. and *Anelosimus eximius*. “Small” spiders were all less than 2 mm in length; “Medium” spiders ranged from 2–4 mm in length, and “Large” spiders were between 4–6 mm in length.

We had sufficient data to look specifically at the distribution of the different size classes and their feeding frequencies for *P. republicana* in the social spider webs. Small *P. republicana* were abundant in the high barrier but a very few were located just above the sheet (Fig. 4). Only 15 of the 172 small spiders we censused captured any prey item and fed during our observations, and the distribution of those individuals was not significantly different from the distribution of all small spiders within the host webs (χ^2 Test, $P > 0.3$) (Fig. 4). Medium-sized *P. republicana* were evenly distributed across the positions within the social spider webs (χ^2 Test, $P > 0.3$); however, those located close to the sheet were more likely to be observed feeding than those in the barrier areas (25 of the 30 spiders that captured prey) (Fig. 4). Forty-seven of the 77 large spiders we observed were located under the sheet of the host web so the distribution of individuals in this size class was not even across the positions (χ^2 Test, $P < 0.05$) (Fig. 4). Twenty-four of the 77 large spiders we censused fed during our observations and 80% of those were located under the sheet (χ^2 Test, $P < 0.05$) (Fig. 4).

Our sample size of *P. republicana* in *Architis* sp. webs was not large enough to make the comparisons of position, size and feeding that we were able to make in the social spider host. Only

5 of the 63 spiders censused in *Architis* sp. webs captured prey, and all of those were spiders in the large size category located in the barrier webbing.

The prey captured by *P. republicana* in these host webs was 2.1 ± 1.2 mm in length which is much smaller than the mean prey size captured by *A. eximius* (5.9 ± 2.1 mm) (Mann-Whitney *U*-Test, $P < 0.05$) (Rypstra 1990). In our prey introduction trials with *Architis* sp., spiders reacted to only 17 of the 112 insects in this size class that we introduced into 10 different webs and the fruit flies were captured on only six occasions. In most of the introductions, the *Architis* web resident did not move at all when the prey were introduced but then would respond to the larger prey item at the end of the trial.

The cribellar silk of the *P. republicana* was able to detain *A. eximius* quite effectively if they happened into one of the webs. On three occasions, a *P. republicana* individual, located in the barrier, successfully captured and killed a penultimate or adult *A. eximius* female. In no case did we observe *A. eximius* capture a *P. republicana*. At dusk, *A. eximius* has a period of web cleaning and maintenance; and, at that time, they would cut out and remove many of the webs of *P. republicana* that were located above the sheet and in the barrier webbing. When they did this, the

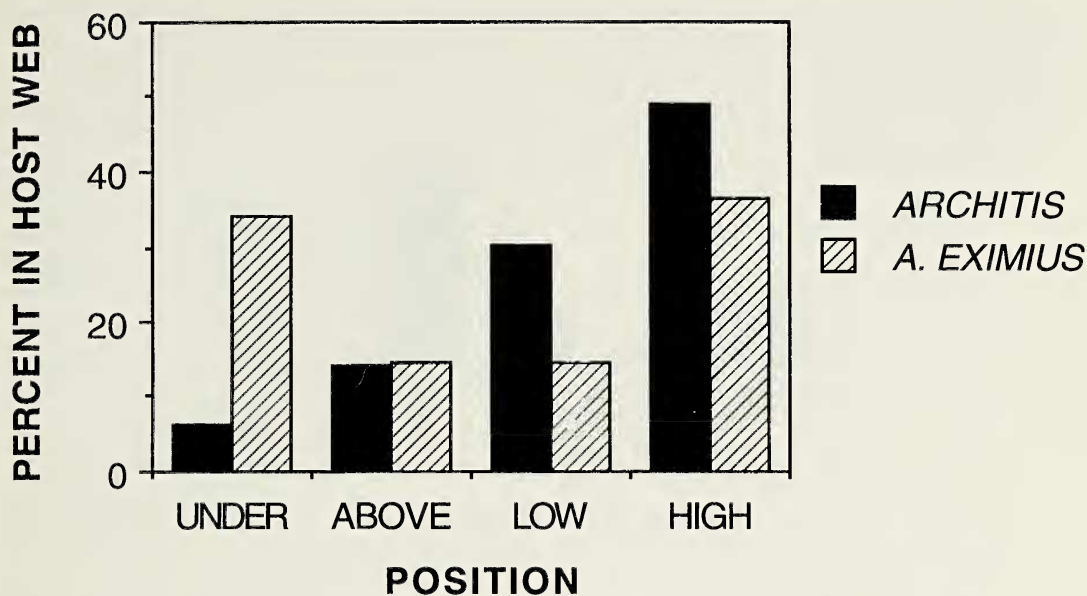


Figure 3.—The distribution of *Philoponella republicana* in the various positions in the host webs. The identified positions were "Under" the sheet, just "Above" the sheet (within 2 cm), in the "Low" barrier webbing (between 2–20 cm above the sheet) and in the "High" barrier (greater than 20 cm above the sheet).

P. republicana would evacuate their web and hang motionless near the location. In only one instance did we observe *A. eximius* destroying a *P. republicana* web located below the sheet during this activity.

DISCUSSION

Our observations suggest that *P. republicana* is a commensal in the webs of *A. eximius* and *Architis* sp. since they capture prey much smaller than those captured by the host species. They appear to use the webs of other species as support, perhaps to enable them to locate their small orb webs in areas otherwise unavailable to them. It is also possible that the webs of the host species enlarge the effective size of their own web allowing them to detect insects sooner and at a greater distance. Perhaps there is some ricochet effect as small insects are deflected and detained by strands of the large host web which could increase the rate of capture by the commensal spider (Uetz 1989). Bradoo (1986) observed *U. ferokus* moving out of their orbs to capture prey on the surface of the host web but we never observed this sort of behavior by *P. republicana*. Bradoo's (1986) descriptions suggest that the relationship between that commensal and its social spider host is much more interdependent than that which

we observed between *P. republicana* and *A. eximius*.

There are more commensals located in the social spider webs than in the solitary spider's web. Likewise, as the social spider web becomes larger more potential web sites are formed and more *P. republicana* colonize them resulting in a correlation between their number and web size. However, even though more web sites would presumably be available as the *Architis* webs increased in size as well, no additional commensal spiders colonized them. We suspect that the increased activity in the social webs deflects more prey into the commensal's webs, which would make those sites preferable. Unfortunately, prey capture by *P. republicana* in *Architis* sp. webs was sufficiently uncommon in our observations that we cannot verify that difference statistically. The fact that there were more large individuals in the social spider webs suggests that they feed more successfully there. In addition, the fact that they are occasional predators on the host in the social spider's web indicates that more potential food is available there.

On the other hand, the density of commensals in the webs of the social spider may not be related to prey capture at all. At some point in the evolution of sociality, spiders must become more tolerant of other spiders (Kullmann 1972; Wil-

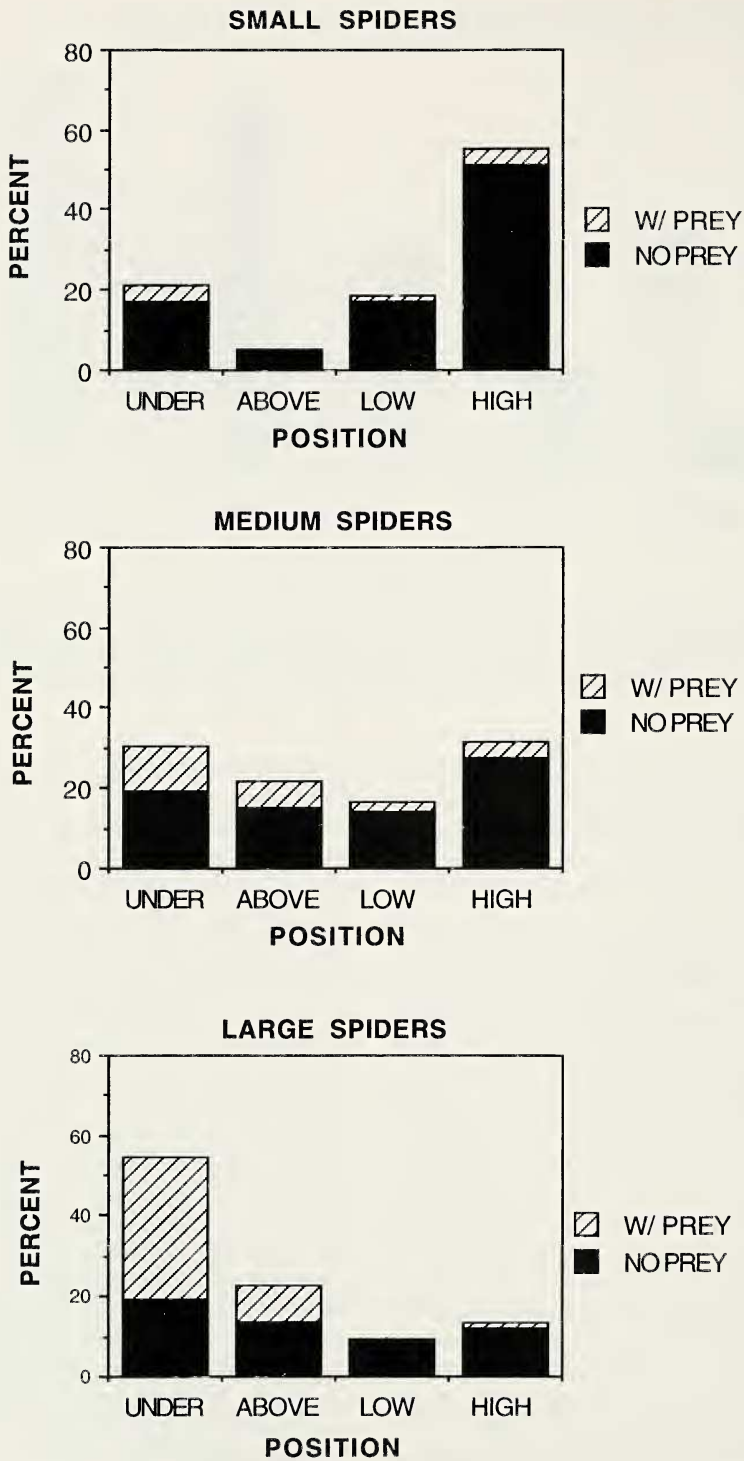


Figure 4.—The distribution of various size classes in the various positions in the social spider webs and the proportion of individuals which were observed to capture prey within a three-hour time period.

son 1975). It may be that *A. eximius* webs are easier to colonize because of this factor. The social spider regularly associates with lots of other spiders and therefore must have relaxed its aggressive tendencies toward them, whereas the solitary species can afford to rid aggressively its web of all other spiders indiscriminately except during the restricted circumstances when it is being courted by a male. The fact that the social species is predisposed to tolerate other spiders may mean that it is easier for heterospecific relationships to perpetuate in their company.

Locations under the sheet in the social spider's webs seem to attract the largest *P. republicana*, and those locations also seem to be the areas of highest prey capture (Fig. 4). It could be that juveniles that happen to select web sites in that location capture more prey and thereby grow large more quickly and/or remain longer in the host web than those in other areas. It is also possible that, as the spiders grow, they are more able to compete for these high quality sites. Our data suggest that sites under the sheet afforded both higher prey capture rates and more protection from disturbance in the host webs of the social spider. One disadvantage to these sites may be that *P. republicana* that located there would encounter fewer of the social spider individuals and therefore be less successful as a predator.

It is curious to note that we never found an adult in the interstices of these complex host webs, even though adults were present in at the study site at the time these data were collected. Interestingly, in our study area we found adults only in aggregations composed exclusively of *P. republicana* individuals. Lubin (1980) suggested that the single species aggregations of *P. republicana* were sibling groups arising from a single egg case, and our surveys of *P. republicana* colonies over the years support that idea (unpub. data). However, we have also observed that a large number of juveniles are commensals for some portion of their life. If this commensal state is a phase that many juveniles pass through, then it would be interesting to discover what cues they use to reaggregate with conspecifics in this complicated habitat. Nyffleler & Benz (1980) report that juvenile stages of several other species of orb weavers act as kleptoparasites and commensals in the webs of other spiders. They consider the commensal relationship as a transition to a more invasive kleptoparasitism. We have already mentioned the more active prey capture out of the host web that Bradoo (1986) reports

for *U. ferokus* which suggests that there is a continuum of dependence on other spider species within the family Uloboridae. It is important to conduct more detailed studies of these relationships in order to understand more fully the evolution of these various behavior patterns.

ACKNOWLEDGMENTS

We thank K. Cangialosi, A. McCrate, S. Tirey, J. Whitis and the staff of the Explorer's Inn for assistance in the field. We are grateful for the cooperation of the staff at the Ministerio de Agricultura de Peru in issuing authorization to work with the spiders of Tambopata. Voucher specimens were placed at the Museo de Historia Natural, Lima, Peru and at the Smithsonian Institution, Washington, D. C. M. A. Hodge and G. W. Uetz made many useful suggestions on an earlier draft of this manuscript. Financial support for this research came from the Society of Sigma Xi, the Frizzell-Exline Fund for Arachnological Research, a Miami University Undergraduate Research Award (all to G. J. B.) and an NSF grant BSR86-04782 (to A. L. R.).

LITERATURE CITED

- Barnard, C. J. & D. B. A. Thompson. 1985. Gulls and Plovers: the Ecology and Behaviour of Mixed-Species Feeding Groups. Columbia Univ. Press, New York, New York.
- Binford, G. J. & A. L. Rypstra. 1992. Foraging behavior of the communal spider, *Philoponella republicana* (Araneae: Uloboridae). J. Ins. Behav., 5:321-335.
- Brach, V. 1975. The biology of the social spider *Anelosimus eximius* (Araneae, Theridiidae). Bull. So. California Acad. Sci., 74:37-41.
- Bradoo, B. L. 1986. Feeding behaviour of a non-poisonous spider *Uloborus ferokus* Bradoo (Araneae: Uloboridae). Zool. Anz., 217:75-88.
- Bradoo, B. L. 1989. Advantages of commensalism in *Uloborus ferokus* Bradoo (Araneae: Uloboridae). J. Bombay Nat. Hist. Soc., 86:232-328.
- Cangialosi, K. R. 1990. Kleptoparasitism in colonies of the social spider *Anelosimus eximius* (Araneae, Theridiidae). Acta Zool. Fennica, 190:51-54.
- Cangialosi, K. R. 1991. Attack strategies of a spider kleptoparasite: effects of prey availability and host colony size. Anim. Behav., 41:639-647.
- Christenson, T. E. 1984. Behaviour of colonial and solitary spiders of the theridiid species *Anelosimus eximius*. Anim. Behav., 32:725-734.
- Erwin, T. L. 1984. Tambopata Reserved Zone, Madre de Dios, Peru: history and description of the reserve. Rev. Peruana Ent., 27:1-8.
- Hodge, M. A. & G. W. Uetz. 1992. Antipredator

- benefits of single- and mixed-species grouping by *Nephila clavipes* (L.) (Araneae, Tetragnathidae). *J. Arachnol.*, 20:212–216.
- Jackson, R. R. 1990. Predator-prey interactions between jumping spiders (Araneae, Salticidae) and *Pholcus phalangioides* (Araneae, Pholcidae). *J. Zool., London*, 220:553–559.
- Jackson, R. R. & M. E. A. Whitehouse. 1986. The biology of New Zealand and Queensland pirate spiders (Araneae, Mimetidae): aggressive mimicry, araneophagy and prey specialization. *J. Zool., London* (A), 210:279–303.
- Kullmann, E. J. 1972. Evolution of social behavior in spiders (Araneae; Eresidae and Theridiidae). *American Zool.*, 12:419–426.
- Lacher, S. R. & D. H. Wise. 1985. Experimental studies of the interactions between a web-invading spider and two host species. *J. Arachnol.*, 13:43–59.
- Lubin, Y. D. 1980. Population studies of two colonial orb-weaving spiders. *Zool. J. Linn. Soc.*, 70:265–287.
- Morse, D. H. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol. Monogr.*, 40: 119–168.
- Nentwig, W. 1985. *Architis nitidopilosa* as a neotropical pisaurid with a permanent catching web. *Bull. British Arachnol. Soc.*, 6:297–303.
- Nyffeler, M. & G. Benz. 1980. Kleptoparasitismus con juvenilen Kreuzspinnen und Skorpionsfliegen in den Netzen adulter Spinnen. *Rev. Suisse Zool.*, 87:907–918.
- Opell, B. P. 1979. Revision of the genera of tropical American species of the spider family Uloboridae. *Bull. Mus. Comp. Zool.*, 148:443–549.
- Pulliam, H. R., & T. Caraco. 1984. Living in groups: Is there an optimal group size? Pp. 122–147, *In Behavioural Ecology: An Evolutionary Approach*. 2nd ed. (J. R. Krebs & N. B. Davies, eds.). Sinauer Associates, Sunderland, Massachusetts.
- Rypstra, A. L. 1979. Foraging flocks of spiders: a study of aggregate behavior in *Cyrtophora citricola* Forskal (Araneae: Araneidae) in west Africa. *Behav. Ecol. Sociobiol.*, 5:291–300.
- Rypstra, A. L. 1990. Prey capture and feeding efficiency of social and solitary spiders: a comparison. *Acta Zool. Fennica*, 190:339–343.
- Rypstra, A. L. & R. S. Tiley. 1991. Prey size, prey perishability and group foraging in a social spider. *Oecologia*, 86:25–30.
- Smith, D. R. R. 1985. Habitat use by colonies of *Philoponella republicana* (Araneae, Uloboridae). *J. Arachnol.*, 13:363–373.
- Struhsaker, T. T. 1969. Notes on the spiders *Uloborus mundior* and *Nephila clavipes* in Panama. *American Midl. Nat.*, 82:611–613.
- Uetz, G. W. 1988. Risk sensitivity and foraging in colonial spiders. Pp. 353–377, *In The Ecology of Social Behavior*. (C. N. Slobodchikoff, ed.), Academic Press, San Diego, California.
- Uetz, G. W. 1989. The “ricochet effect” and prey capture in colonial spiders. *Oecologia*, 81:154–159.
- Uetz, G. W. & C. S. Heiber. 1994. Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. *Behav. Ecol.*, 5:326–332.
- Vollrath, F. 1987. Kleptobiosis in spiders. Pp. 274–286, *In Ecophysiology of Spiders*. (W. Nentwig, ed.) Springer-Verlag, Berlin.
- Wilson, E. O. 1975. *Sociobiology – The new synthesis*. Harvard Univ. Press, Cambridge, Massachusetts. 697 pp.

Manuscript received 26 November 1994, revised 1 December 1994.